

remains of a nest with fragments of shells was discovered, we saw no sign of a living bird. The stupid tameness of this species threatens its extermination, unless it is able to retain a footing on the east side. Possibly the open winter of 1920-21 with the comparative absence of snow, induced the birds to leave their old haunts and migrate to fresh fields, unless, indeed, it has been locally exterminated.

IX.—*Species and Subspecies*.

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ONE of the chief reasons which induced me, in collaboration with Mr. Mackworth-Praed (*Ibis*, 1921, pp. 344-347), to chase the hare started by Mr. Loomis in the pages of 'The *Ibis*' (1920, pp. 964-966) on the subject of subspecies, was to call attention to the opinion held by us, that ornithologists in general did not apparently sufficiently distinguish between mutational or discontinuous variations which characterised one form of subspecies and continuous or environmental variations which characterised another form.

If I may venture, in flat defiance of the example of the angels, to plunge once more into the discussion, I would like to give one or two concrete examples by way of illustrating what are my own personal views on the matter.

A. As examples of discontinuous or mutational subspecies I may quote the following, taken at random:—

- (1) *Pluvialis apricarius oreophilus* Meinertz, which has just recently been described (*Bull. B. O. C.* vol. xlii. 1921, p. 6).
- (2) *Podiceps cristatus infuscatus* Salvad.
- (3) *Querquedula discors albinucha* Kennard, *Auk*, xxxvi. 1919, pp. 459-460.

Examining these in detail and confining myself to a single differential character in each, we find that:—

In *Pluvialis a. oreophilus* the narrow but well-defined black frontal band present in *P. a. apricarius* is absent in the British breeding race (*cf.* *Bull. B. O. C. loc. cit.*).

In *Podiceps cristatus infuscatus*, as pointed out by Mr. Claude Grant (Ibis, 1915, p. 51), the white superciliary streak present in *P. c. cristatus* (Europe) is absent in the African race, a character which is as noticeable in winter as in summer dress. This is well illustrated in a woodcut accompanying the article.

Querquedula discors albinucha is similar to *Q. d. discors* except that, in the nuptial plumage of the male, the crescentic white patch in front of the eye is continued over the eye in a thin superciliary line down to the nape, where it meets the line from the opposite side to form a white nuchal patch.

This Teal breeds commonly in Louisiana, possibly as far east as Florida, also in Texas and Mexico, and begins nesting before the Blue-winged Teal departs for the north.

A good illustration is given in the reference quoted above.

In these examples, then, we find that the race, variety, or subspecies—call it what you will—differs from the typical species in the presence or absence of well-marked colour-pattern characters. We find that certain qualitative changes or characters have been introduced. The fact that they are small differences does not matter in the least; for the important point about them is that they are definitely and obviously heritable characters, which, by no stretch of the imagination, can be conceived of as co-related with adaptation.

The case of the Louisiana Teal is particularly interesting, as the character has apparently not as yet been completely and permanently established. To be so definitely and concisely repeated in succeeding generations there is only one conceivable way by which such characters could have originated; there must have been some change, some "jugglery"—call it what you will—initiated *de novo* in the chromosomes or chromomeres, or at any rate in the fertilised ovum. Moreover, for the continued presence, or the continued absence, of such mutational characters in such differentiated races the only possible explanation would

seem to be, that, having once arisen, they were able to persist by virtue of this gametic origin plus the additional fact that they occurred in isolated geographical populations, or in populations whose breeding-seasons did not synchronise with those of the typical race. Furthermore, not being blatantly or obviously out of harmony with their surroundings they were "good enough," and there was no obvious excuse for Natural Selection to interfere.

To regard such colour-pattern mutations as having been directly initiated and gradually perfected by any form of environmental influence seems to denote little more than a simple faith in a purely theoretical conception, for which almost untold ages and far too great a strain on the scientific imagination are necessary. It seems equally inconceivable to regard them as having arisen in response to any adaptive call, although to make this assertion is not to deny that many colour-patterns may be adaptive.

Mr. Stuart Baker, in a highly interesting and important revision of the genus *Gemmæus* (Journ. Bombay Nat. Hist. Soc. xxiii. 1915, pp. 658-689), calls attention to the three dominant types of colour-pattern in this group of pheasants, obtaining respectively in *G. horsfieldi*, *G. lineatus*, and *G. nycthemerus*, and dwells upon the fact that the obviously contrasted differences in colour-pattern of the three forms are directly due to three different forms of environment. I find it as equally impossible to regard the beautifully etched vermiculations on the dorsal surface of *G. lineatus* as having originated in either direct or indirect response to the type of environment described as "hills of moderate height covered with mixed forest, bamboos, and grass land, with a moderate rainfall" (the last in contradistinction to "a heavy rainfall" in the case of *G. horsfieldi*), as to believe that the peculiar physiognomy of Neanderthal man arose in response to anything co-related with the physical environment to which he was exposed in Pleistocene Europe. It is, I imagine, as certain as anything can be, that Neanderthal man owed his physical features to a complex of factors which he inherited in the only way we know

of, from his forbears, human and otherwise; and I believe it is as certain that the finely vermiculated markings of *G. lineatus* were derived in like manner from its various progenitors. It is important to dwell upon these points in order to make evident the differences between mutational and environmental subspecies. It seems well-nigh inconceivable, even as an abstract proposition, to picture Natural Selection seizing upon a small favourable variation here and another there, in the direction of fine vermiculations which harmonised with the immediate environment, and finally building them up into the perfect article by the elimination of the unfavourable variations*. Consider for a moment the various types of environment to which *Phasianus colchicus* has been exposed for a thousand years in the British Isles.

We know that the old English Pheasant was introduced from the banks of the river Phasis in Colchis (hence the name *Phasianus colchicus*), and very probably by the Romans (*cf.* Newton's 'Dictionary of Birds'). Are we to believe that the environmental conditions obtaining in southern Russia are so precisely identical with those in the British Isles that in a thousand years or more no perceptible change in colour-pattern would have been brought about; or was it not more likely that the "English Pheasant" remained unchanged, and would have continued to remain unchanged, homozygous as every individual was, until crossed with newly introduced races from still farther east, such as the Ring-neck?

"Pure-bred" as *P. colchicus* was when introduced by the Romans, I cannot but believe that it would have remained "pure-bred" to the last if it had been left alone, since there is no evidence that there was any innate tendency to variation in its constitution, or any very likely natural facilities for adequately isolating such variations if they arose.

* NOTE.—On the contrary, there would appear to be little doubt that *G. lineatus*, along with most of the subspecies of the genus *Gemnaeus* which have been described from Burma and adjacent countries, is a mendelian segregate, and the most likely explanation of its origin would appear to have been a crossing between two such forms as *G. horsfieldi* and *G. nyctemerus* (*cf.* J. C. Phillips, 'Genetics,' vi. 1921, p. 376).

By the phrase "remaining unchanged" I am not, of course, referring to mere depth of colour-tones produced by chemical processes in the pigment contained in the feathers as the result of external climatic agencies, but to actual differences in colour-pattern.

But to return once more to the examples of specific variation which we have quoted at the outset of these remarks, and which have appeared to me to be convenient examples of what may be termed mutational subspecies as opposed to environmental, there would undoubtedly seem to be a practical difficulty in the matter of nomenclature in connection with them. For if we roundly regard them as "species" our nomenclature will fall short of indicating (as trinomials do so conveniently) their undoubted genetic relationships to the typical races—*Podiceps cristatus infuscatus*, for instance, being undoubtedly genetically allied to *P. c. cristatus*.

My meaning may be rendered clearer by what immediately follows.

Mr. Bonhote in his letter to 'The Ibis' on "Subspecies and their part in Evolution" (Ibis, 1921, p. 721) writes, as follows:—"I had always understood that a true subspecies was always supposed to be restricted to the latter cause [*i. e.* environment], and certainly think it should be so." This may be so or not; certainly it is not followed out in practice by the majority of systematists; but if it is so, it follows that Mr. Bonhote would either consider that the examples I have quoted owe their origin to environmental causes (an opinion which with his experience of breeding mammals and birds I should hesitate to attribute to him), or that they are not "true subspecies," and that in so writing them down systematists have erred. If this latter conclusion is correct, the question at once arises, *what are they?* The question is a practical one, apart from the more deep-seated one which underlies our recognition that this kind of subspecies differs from a purely environmental subspecies, such, for example, as a dark form originating in a damp humid climate.

The only solution which occurs to me at the present

moment would be to call them "geographical species." The name is one which is accurately descriptive, and it brings out the fact that such specific variations have "equal rank" with "species"—that they might be, in fact, regarded as "species," even using that word in its nomenclatural and systematic sense, and not *subspecies*. For it may not be needless to point out that we have no knowledge to guide us to a conclusion as to whether, for example, the European race of Great Crested Grebe was differentiated prior to the differentiation of the African, or *vice versa*, or whether they were differentiated simultaneously from a common type. The solution perhaps lies rather in the probability that there was an extension of range from one continent to the other with subsequent differentiation in the new area occupied—but this by the way.

For, in passing on, there is another point which I should like to dwell on, viz., that if there is any excuse whatever for regarding subspecies as "incipient species" we must surely confine such a term to the kind of "subspecies" which I have been discussing, and by no manner of means to the kind which Mr. Bonhote refers to as a "true or environmental subspecies"; for since in an "environmental subspecies" it is only the soma which is affected, unless one believes in the inheritance of acquired characters it is difficult, nay impossible, to conceive how such subspecies can play any part in the generally accepted scheme of evolution. But granting this as approximating very nearly to what is almost universally held to be the truth, we arrive at the consideration of our second group (viz. B. Environmental subspecies), and find that it is mostly comprised of numbers of trinomialised variations for which some such description as the following might very well be taken as a standard:—

"— — — differs from typical examples in being of a distinctly darker shade of ——— on the mantle and coverts, in being slightly paler below, and in having the wing and tail measurements averaging — mm. longer or shorter," the variation obviously being the direct result of a more humid, more arid, more sunlit, more sunless, or more or less adjectival locality.

Of this kind of variation, and I am not doubting the utility of their recognition so long as we do it wisely, numerous examples will occur at once to anyone engaged in the work of systematic ornithology. I would suggest the Paridæ for consideration as the first group to occur to me; but would more particularly notice an example which I have already alluded to elsewhere.

In the Bermudas, the Goldfinch (*Carduelis carduelis*) would appear to have established itself in the islands somewhere about the year 1875, cage birds having apparently been introduced either from the Canaries or Europe. It would now appear to be of a darker shade of coloration on the upper parts than typical examples, and for this reason has been separated by Mr. Kennedy as a subspecies under the name of *C. carduelis bermudiana*. In point of fact, it is "as good a subspecies" as scores of others now recognized by all of us. But my point is that this darker coloration is purely a quantitative somatic change due to chemical or actinic factors in the environment, and consequently would not be inherited; so that if the bird were transported to its original habitat the coloration would revert to its former tones. In this respect, if my contention is true, it differs fundamentally from the case of any of the examples which I have quoted as characteristic of "mutational subspecies" or "geographic species."

Want of space forbids my enlarging on this subject by continuing to quote further examples or to allude to the vexed question of intermediate and island forms, many of which last are undoubted subspecies.

The whole subject is further complicated by the fact that in any given subspecies one may meet with purely somatic or environmental characters superimposed upon mutational or gametic characters. To attempt to deal in anything like an adequate way with such a difficult problem as the whole question of subspecies and their classification involves, is impossible at the present time; but these few lines are written in a tentative spirit in the hope that they will lead to concentration of thought along the lines indicated.